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Studies on Retranslocation of Accumulated Assimilates in 'Delaware' Grapevines

I. Retranslocation of ^{14}C-assimilates in the Following Spring after ^{14}C Feeding in Summer and Autumn

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Summary

Potted 'Delaware' grapevines were supplied with $^{14}CO_2$ in the summer and autumn respectively, and the accumulation and retranslocation of ^{14}C-assimilates were investigated from the pruning time to the flowering and the young berry stages of the newly developed shoots in the following spring.

At pruning time, ^{14}C-assimilates were distributed to the roots in a higher ratio than to the trunk and canes, and this trend was more marked for the autumn than for the summer feeding. The respiratory consumption and retranslocation of ^{14}C throughout the new shoot growth were evaluated as percentages of ^{14}C having been found in the vine just after pruning. The percentage respiratory consumption of ^{14}C was evidently higher for the autumn feeding. Retranslocation began with the bud burst, reached a maximum at the 6- to 8- leaf stages and the 10-leaf stage respectively for the autumn and summer feedings and then ceased by the flowering stage. Such a time course of retranslocation was recognized also by radioautographs of the new shoot and especially of the shoot apex. The maximum percentage retranslocation was 5.1–5.2 and 15.3–10.7 for the summer and autumn feedings respectively. The distribution of ^{14}C among chemical fractions was also measured in the roots, trunk and new shoots. It was peculiar to the new shoots that nearly half of their ethanol soluble ^{14}C was found in the amino acids unlike the one-sided distribution to soluble carbohydrates in the trunk and roots. It seemed that amino acids were retranslocated to the new shoots after being synthesized in the roots.

In most deciduous fruit trees, sufficient accumulation of photosynthetic assimilates and their active retranslocation are important to secure a vigorous early growth of the new shoots in the following spring. Especially in grapevines, in which the differentiation and development of flower organs proceed after the bud burst, the importance of retranslocated assimilates on fruitfulness has been greatly emphasized, but sufficient data is lacking on the retranslocation from the quantitative viewpoint. In addition, in the grape culture in the Tohoku district, where leaf-fall occurs earlier in autumn, the limited duration of photosynthesis and

the resultant insufficient accumulation of the assimilates are considered to decrease cold hardiness in winter as well as the early growth of the new shoots in the following spring.

We are now carrying out serial experiments with 'Delaware' grapevines and making use of ^{14}C not only to evaluate the accumulation and retranslocation quantitatively, but also to investigate the importance of retranslocated assimilates on the new shoot growth in relation to the current year assimilates of the new shoots themselves. In addition, we intend to supplement the results obtained with ^{14}C by analysing the dynamic status of the total carbon in each plant part. In this report, the grapevines were supplied with $^{14}CO_2$ in summer and autumn respectively, and the distribution of accumulated ^{14}C in the vine as well as the time course and magnitude of retranslocation of ^{14}C in the following spring were measured. In addition, the distribution of ^{14}C among chemical fractions was examined on each plant part.

Materials and Methods

Experiment I.

Three-year-old cuttings of 'Delaware' grapevines (*Vitis labruscana* Bailey) were cut back to six buds and planted into 30-cm pots in March, 1974. In the growing season, two shoots were left to grow and topped leaving ten leaves on each shoot. Only one flower cluster on the upper shoot was allowed to develop, and the other clusters and all the axillary shoots were removed as soon as possible. These vines were divided into two groups and the middle leaf (the fifth leaf from the base) of the lower shoot on each individual vine was supplied with 40μ Ci $^{14}CO_2$ on July 27 (summer) and September 5 (autumn) respectively. On January 25, 1975, the lower cane was pruned off, while the upper one was cut back to six buds, among which two were left to grow in the spring and treated as in the previous season. Two vines in each group were sampled three times sequentially on January 25 (the dormant stage), June 16 (the flowering stage) and July 9 (the young berry stage), and severed rapidly into several component parts. They were, then, air-dried, weighed and pulverised for the determination of ^{14}C radioactivity.

In addition, the distribution of ^{14}C among the chemical fractions was determined on each plant part. Two hundreds mg of dried material was extracted with hot 80 per cent (v/v) ethanol. The ethanol extracts were passed through columns of cation and anion exchange resins (Amberlite IR-120 and IR-4B) in order. The eluants from the cation column contained amino acids, and from the anion column organic acids, whereas the neutral effluents contained soluble carbohydrates. ^{14}C radioactivity of these three fractions together with of the ethanol insoluble fraction were determined by liquid scintillation spectrometry.

Experiment II

Three-year-old cuttings of 'Delaware' grapevines, grown as in Experiment I but with no flower cluster developed, were used. On July 29 and September 17, 1976, respectively, two leaves (the fifth and sixth leaves from the base) of the upper shoot on each individual vine were supplied with 40 μ Ci $^{14}CO_2$ instead of a single leaf on the lower shoot in Experiment I. On October 16, the fed vines were pruned as in Experiment I, and two buds of the upper cane were allowed to develop in the following spring. On October 16 (the leaf-fall stage), January 25 (the dormant stage), April 13 (before the bud burst), May 20 (the 6-leaf stage), June 1 (the 8-leaf stage), June 8 (the 10-leaf stage) and June 17 (the flowering stage) three vines in each group were sampled, severed and air-dried as in Experiment I.

Besides the determination of retranslocation, the distribution of ^{14}C within the newly developed shoots was examined by radioautography. For that purpose, extra vines having been fed in autumn were used, and each vine was sampled eight times sequentially from the 3- to 10-leaf stages. The shoots were pressed and dried, then mounted on the Fuji X-ray films, which were exposed for three weeks and then developed. In addition, the RSS (mentioned below) of the shoot apex was measured with the same shoots as used for radioautography.

General Procedures of Feeding, Determination of Radioactivity and Calculation of the Results.

Feeding of $^{14}CO_2$: The fed leaf or leaves were enclosed in a polythene bag, into which $Na_2{}^{14}CO_3$ solution and 20 per cent (v/v) lactic acid were poured separately, and then mixed to generate $^{14}CO_2$. The leaves were exposed for one hour from 10.00 to 11.00 hour under natural daylight on sunny days without temperature control.

Measurement of ^{14}C radioactivity: Twenty mg of dried material was oxidized by combustion using a Packard sample oxidizer. The generated $^{14}CO_2$ was absorbed into 4 ml of Carbo-sorb, to which 9 ml of scintillator, Permaflow V, was added and counted for ^{14}C radioactivity in a Packard liquid scintillation spectrometer. The counting efficiency was always over 80 per cent.

Calculation and Representation of the Results: The results were expressed as percentage total export, percentage distribution, percentage retranslocation and RSS (Relative strength as a sink), which were calculated as follows.

Percentage total export from the fed leaf or leaves =(^{14}C recovered in a whole plant except the fed leaves/Total ^{14}C recovered)$\times$100

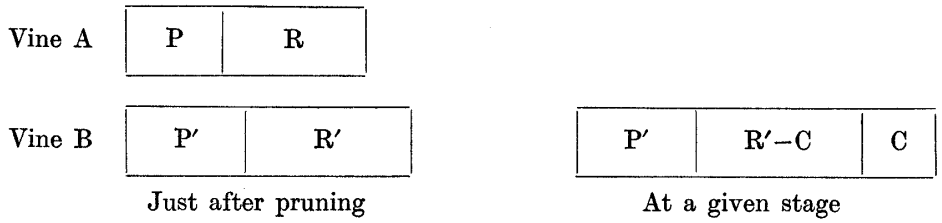
Percentage distribution to each plant part =(^{14}C recovered in each plant part/Total ^{14}C recovered in all the plant parts as sinks)$\times$100

Percentage retranslocation to the newly developed shoots=(^{14}C recovered in the new shoots/^{14}C recovered in a whole plant just after pruning)$\times$100

RSS=(Specific activity of ^{14}C in each plant part/Specific activity of ^{14}C of a plant as a whole)$\times$100=(Percentage distribution of ^{14}C to each plant part / Percentage

distribution of dry matter to each plant part; the fed leaves being excluded)×100

In the calculation of percentage retranslocation, there is nothing but to use different vines sampled at different times for the evaluation of numerator and denominator. Then, for that procedure, it goes without saying that the amount of ^{14}C absorbed at the feeding time should be the same among the vines used. Unfortunately, it was not the case because of some technical difficulties, which made the direct calculation impossible. Percentage retranslocation, however, could be calculated indirectly by the procedure described in Figure 1, taking



P, P′: ^{14}C recovered in the pruned-off parts of the vine; having no consumption by respiration because the plant parts were dried immediately after harvest.
R, R′: ^{14}C recovered in the vine just after pruning.
C: ^{14}C consumed in respiration for the period from pruning to a given stage.
P, P′, R and R′−C: Measurable.
In the figures mentioned above,

$$a=R/(P+R)=R'/(P'+R') \quad (1)$$

$$b=(R'-C)/(P'+(R'-C)) \quad (2)$$

From (1) and (2),

$$C=(a-b)R'/a(1-b)$$

$$R'-C=(1-a)bR'/a(1-b)$$

Then, when expressed as percentages of R′,

Percentage respiratory consumption of $^{14}C=(a-b)\times 100/a(1-b)$

Percentage ^{14}C remaining in the vine$=(1-a)b\times 100/a(1-b)$

When S (R′−C) is found in the newly developed shoots,

Percentage retranslocation$=(1-a)bS\times 100/a(1-b)$

FIG. 1. How to calculate percentage respiratory consumption and percentage restranslocation (Indirect calculation).

advantage of the fact that there was little difference among vines in the ratio of the amount of ^{14}C recovered in the fallen leaves and pruned-off canes to that recovered in a whole plant just after pruning. In addition, it must be noted that in the calculation mentioned above, the respiratory consumption of ^{14}C was neglected, then, the percentage retranslocation in our terminology is of net or apparent value based on the amount of ^{14}C recovered in a whole plant just after pruning and not just after feeding.

Results

Accumulation of ^{14}C-assimilates.

In both Experiment I and II, the percentage total export of ^{14}C at the pruning time was higher for the summer than for the autumn feeding; being 80–75 per cent

and 68–69 per cent respectively. Of the total export of ^{14}C, 50–53 per cent and 77–84 per cent were distributed to the roots for the summer and autumn feeding respectively, and the remainders to the trunk, canes, fallen leaves and fruit cluster, though only little to the latter two (fruit cluster being included only in Experiment I). In the vine just after pruning as much as 94–98 per cent of the total export of ^{14}C was found, with an exception of 78 per cent for the summer feeding in Experiment I, where much of ^{14}C was distributed to the lower cane which had been pruned off. Within the vine just after pruning, much of ^{14}C was distributed to the roots, next to the trunk and then to the cane, except for the summer feeding in Experiment II. The high percentage distribution to the roots was especially marked for the autumn feeding, and for the summer feeding in Experiment II more ^{14}C was found in the cane than in the trunk (Table 1 and 2).

TABLE 1. *Total Export and Distribution of ^{14}C within Vines just before and after Pruning in Relation to the Feeding Time (Exp. I)*

Feeding time	Total export (%)	Distribution just before and (after) pruning[z] (%)					
		Fallen leaves	Canes pruned-off	Cane	Trunk	Roots	Total
Summer[y]	80.3	4.4[w]	17.5	0.6 (0.8)	27.8 (35.6)	49.7 (63.6)	100 (100)
Autumn[x]	67.6	1.3	4.7	0.2 (0.2)	16.9 (18.0)	76.9 (81.8)	100 (100)

z: January 25, 1975. y: July 27, 1974.
x: September 5, 1974. w: Fruit cluster included.

TABLE 2. *Total Export and Distribution of ^{14}C within Vines just before and after Pruning in Relation to the Feeding Time (Exp. II)*

Feeding time	Total export (%)	Distribution just before and (after) pruning[z] (%)					
		Fallen leaves	Canes pruned-off	Cane	Trunk	Roots	Total
Summer[y]	75.4	1.2	0.8	26.1 (26.7)	19.2 (19.6)	52.7 (53.7)	100 (100)
Autumn[x]	68.8	0.9	0.4	5.5 (5.6)	9.5 (9.6)	83.7 (84.8)	100 (100)

z: October 16, 1976. y: July 29, 1976. x: September 17, 1976.

Time Course and Magnitude of Retranslocation.

In Experiment I, 18–24 per cent and 43–66 per cent of ^{14}C having been found in the vine just after pruning were consumed perhaps in respiration at the flowering and young berry stages respectively, and the respiratory consumption was larger for the autumn than for the summer feeding. The percentage retranslocation of ^{14}C at the flowering stage was evidently higher for the autumn feeding; being 5.1 and 15.3 per cent for the summer and autumn feeding respectively. From the

flowering to the young berry stage, however, it decreased to 4.2 and 6.3 per cent respectively perhaps due to the decrease of true retranslocation and the increased respiratory consumption. The respiratory consumption in each plant part during a given period such as between (a) and (b) in Table 3 could be tentatively obtained by apportioning the respiratory consumption as a whole among the plant parts assuming that the respiration rate was the same for all the parts and the mean value of the percentage distribution at (a) and (b) was taken for the size of the substrates for respiration. When the respiratory consumption in each part was evaluated, it was easy to get the true incoming or outgoing into or from each part, and they were shown in brackets in Table 3 and 4 together with the respiratory consumption. Thus, the incoming into the newly developed shoots for the period from pruning till the flowering stage was 5.6 and 17.3 per cent, respectively, for the summer and autumn feeding. For the period from the flowering to the young berry stage, however, it decreased to 0.7 and 0.1 per cent respectively (Table 3).

TABLE 3. *Distribution of the Summer and Autumn Assimilated ^{14}C within Vines in Relation to the Development of New Shoots in the Spring, Expressed as Percentage of ^{14}C Found in the Vine just after Pruning (Exp. I)*

Feeding time	Plant part	Harvest date			Respiratory consumption (left) and true incoming or outgoing (right) into or from each plant part[w] during a given period			
		Jan. 25 Just after pruning (a)	June 16 Flowering stage (b)	July 9 Young berry stage (c)	(a) ~ (b)		(b) ~ (c)	
Summer[z]	New shoots	—	5.1[x]	4.2[x]	−0.5	+5.6	−1.6	+0.7
	Cane	0.8	0.9	0.6	−0.2	+0.3	−0.3	0
	Trunk	35.6	26.1	20.9	−6.2	−3.3	−8.3	+3.1
	Roots	63.6	49.7	31.5	−11.3	−2.6	−14.4	−3.8
	Whole plant	100	81.8	57.2	−18.2	0	−24.6	0
Autumn[y]	New shoots	—	15.3[x]	6.9[x]	−2.0	+17.3	−8.5	+0.1
	Cane	0.2	0.5	0.2	−0.3	+0.6	−0.3	0
	Trunk	18.0	7.8	2.9	−3.4	−6.8	−4.1	−0.8
	Roots	81.8	52.3	23.9	−18.4	−11.1	−29.1	+0.7
	Whole plant	100	75.9	33.9	−24.1	0	−29.1	0

z : July 27, 1974.
y : September 5, 1974.
x : These figures correspond to percentage retranslocation.
w: Tentatively calculated. +: Incoming, −: Outgoing or consumed.

As it appeared from Experiment I that the retranslocation was almost stopped by the flowering stage, Experiment II was designed to investigate in detail the situation at early stages prior to flowering. The respiratory consumption as a whole during the period from pruning till the flowering stage was 30 and 46 per cent for the summer and autumn feeding respectively, showing a trend similar to that of

Experiment I, except that it was somewhat higher due to the difference of the time of pruning. For the autumn feeding, the percentage retranslocation reached a maximum as early as the 6- to 8-leaf stages (10.6–10.7 per cent) and thereafter till flowering almost no change was found. The incoming into the new shoots during the period from pruning till the 6-leaf stage was 11.0 per cent, while that from the 6-leaf till the flowering stage was only 2.1 per cent. For the summer feeding, the maximum percentage retranslocation was 5.2, which was attained at the 10-leaf stage, later than for the autumn feeding. The incoming into the new shoots during the period till the 10-leaf stage was 5.4 per cent, while thereafter some outgoing was found, though only a little. In addition, for the summer feeding, in which much of ^{14}C had accumulated in the cane, retranslocation seemed to occur first from the cane, then from the roots and trunk, and the magnitude of retranslocation also seemed to be higher from the cane than from the roots and trunk (Table 4).

Distribution of ^{14}C within the Newly Developed Shoot.

Both in Experiment I and II, much of the ^{14}C in the newly developed shoot was distributed to the leaves and stem, but little to the cluster and shoot apex irrespective of the growth stage or the feeding time. The small distribution to the cluster and shoot apex was due to the low percentage distribution of dry matter to them (Fig. 2, 3).

In Experiment I, the RSS values were high in the lower stem and leaves and decreased in the apical ones through the flowering to young berry stages. While the cluster, which was opposite to the fourth leaf, had a fairly high value appropriate to its position on the stem at the flowering stage, but it decreased rapidly towards the young berry stage (Fig. 2). In Experiment II, the RSS values at the 6-leaf stage were about 100 and there was little difference among the cluster, stem and

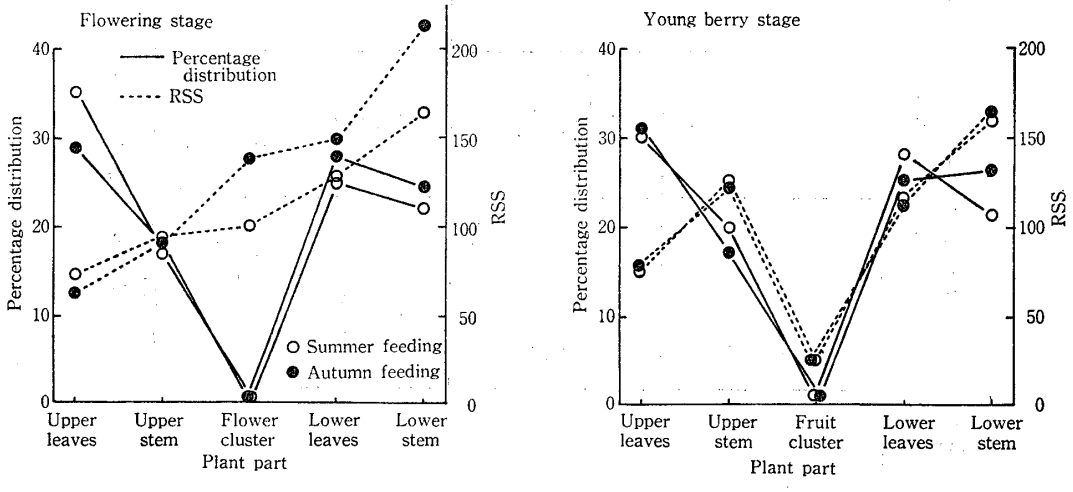


FIG. 2. Percentage distribution of retranslocated ^{14}C and sink activity within the newly developed shoot at the flowering stage and the young berry stage (Exp. I).

TABLE 4. *Distribution of the Summer and Autumn Assimilated ^{14}C within Vines in Relation to the Development of New Shoots in the Spring, Expressed as Precentage of ^{14}C Found in the Vine just after Pruning (Exp. II)*

Feeding time	Plant part	Harvest date							Respiratory consumption (left) and true incoming or outgoing (right) into or from each plant part[w] during a given period
		Oct. 16 Just after pruning (a)	Jan. 25 Dormant stage (b)	Apr. 13 Before bud burst (c)	May 20 6-leaf stage (d)	June 1 8-leaf stage (e)	June 8 10-leaf stage (f)	June 17 Flowering stage (g)	
									(a) ~ (f)
Summer[z]	New shoots	—	—	—	2.8[x]	3.1[x]	5.2[x]	4.5[x]	−0.2 +5.4
	Cane	26.7	21.8	17.2	11.4	14.1	12.8	15.3	−6.1 −7.8
	Trunk	19.6	20.8	21.1	20.5	20.5	16.8	16.8	−6.3 +3.5
	Roots	53.7	45.3	40.9	43.1	38.6	38.8	34.0	−13.8 −1.1
	Whole plant	100	87.9	79.2	77.8	76.3	73.6	70.6	−26.4 0
									(a) ~ (d)
Autumn[y]	New shoots	—	—	—	10.6[x]	10.7[x]	9.3[x]	10.6[x]	−0.4 +11.0
	Cane	5.6	4.6	3.5	3.8	2.3	1.6	1.7	−1.6 −0.2
	Trunk	9.6	13.0	5.4	8.1	2.6	3.4	2.5	−3.8 +2.3
	Roots	84.8	72.7	62.8	44.5	46.9	43.7	39.0	−27.2 −13.1
	Whole plant	100	90.3	71.7	67.0	62.5	58.0	53.8	−33.0 0

z: July 29, 1976.
y: September 17, 1976.
x: These figures correspond to precentage retranslocation.
w: Tentatively calculated. +: Incoming, −: Outgoing or consumed.

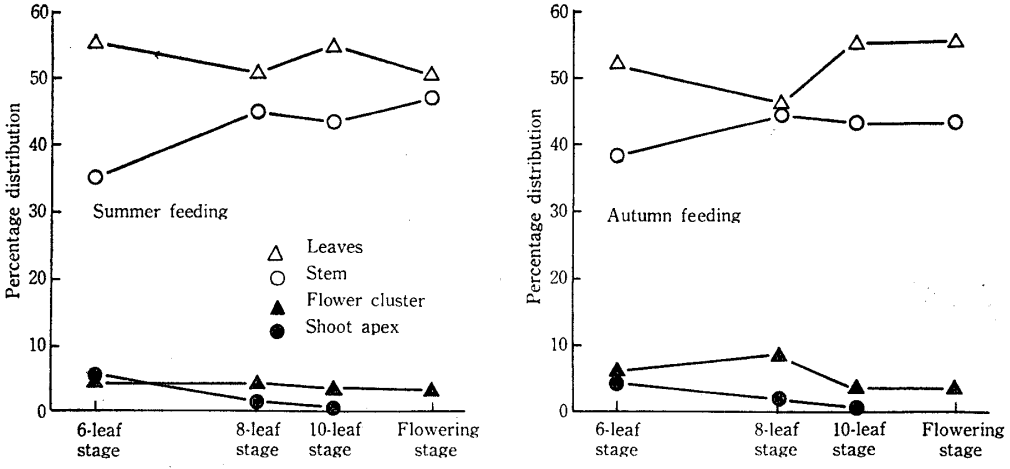


FIG. 3. Percentage distribution of retranslocated ^{14}C within the newly developed shoot in relation to its development and to the feeding time (Exp. II).

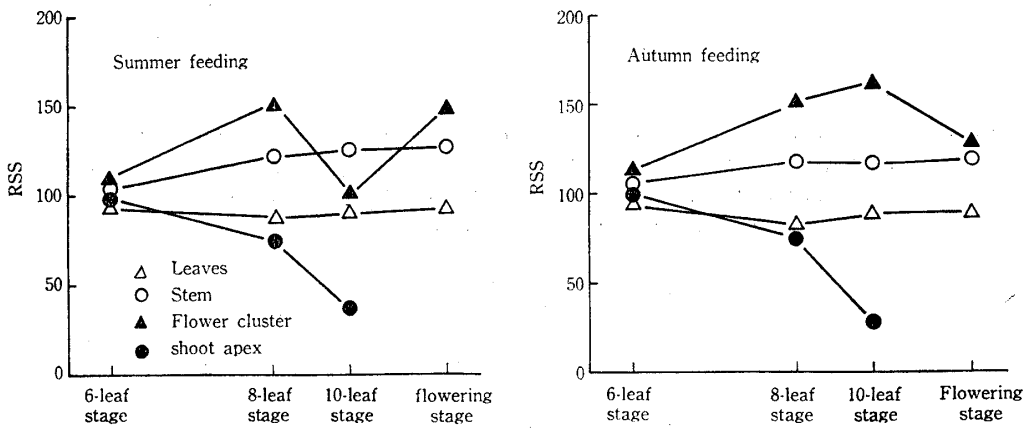


FIG. 4. Sink activity within the newly developed shoot in relation to its development and to the feeding time (Exp. II).

leaves. At and after the 8-leaf stage, they were within the range 150–80 for the cluster, stem and leaves in descending order, and such values were kept until the flowering stage. For the shoot apex, however, the value began to decrease at the 8-leaf stage and reached as low as 40 at the 10-leaf stage (Fig. 4).

In Experiment II, the distribution of retranslocated ^{14}C within the newly developed shoot was examined also by radioautography. At the 3- to 5-leaf stages, ^{14}C radioactivity was found in high concentrations in a whole shoot, and especially in the stem, veins and clusters. From the 6-leaf stage it decreased gradually, and concomitantly, there appeared a clear concentration gradient which was lower at the upper parts. Especially in the shoot apex, radioactivity became faint at the 8-leaf stage and at the 10-leaf stage there was almost no activity (Plate 1). A similar trend could be found in Figure 5 showing RSS values of the shoot apex obtained with the same materials as used for radioautography.

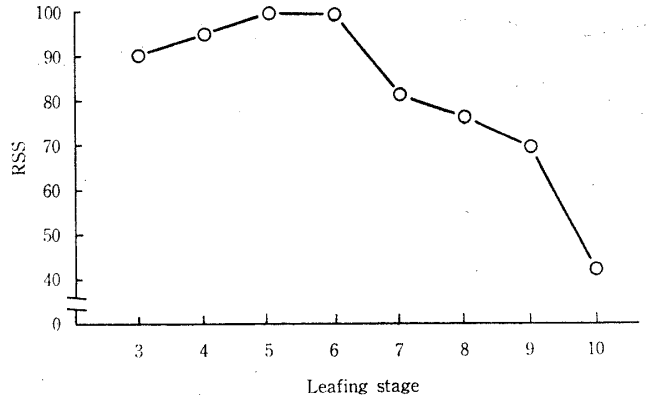


FIG. 5. Sink activity of shoot apex in relation to the development of the new shoot after $^{14}CO_2$ feeding in the previous autumn (Exp. II).

Distribution of ^{14}C Among Chemical Fractions in Each Plant Part.

At the pruning time, 31 and 36 per cent of the ^{14}C in the roots was found in the ethanol soluble fraction for the summer and autumn feeding respectively. In the

TABLE 5. *Distribution of ^{14}C in Each Plant Part among the Ethanol Soluble and Insoluble Fractions and within the Ethanol Soluble Fraction among Soluble Carbohydrates, Amino Acids and Organic Acids in the Vines just after Pruning (Exp. I)*

Feeding time	Plant part	Ethanol insoluble	Ethanol soluble	Within ethanol soluble fraction		
				Soluble carbohydrates	Organic acids	Amino acids
Summer	Trunk	83.0	17.0	85.5	7.8	6.7
	Roots	68.8	31.2	93.5	3.0	3.5
Autumn	Trunk	56.4	43.6	86.4	5.7	7.9
	Roots	63.9	36.1	87.6	3.3	9.1

TABLE 6. *Distribution of ^{14}C in Each Plant Part among the Ethanol Soluble and Insoluble Fraction and within the Ethanol Soluble Fraction among Soluble Carbohydrates, Amino Acids and Organic Acids in the Vines at the Flowering stage (Exp. I)*

Feeding time	Plant part	Ethanol insoluble	Ethanol soluble	Within ethanol soluble fraction		
				Soluble carbohydrates	Organic acids	Amino acids
Summer	New shoots	83.4	16.6	32.3	9.9	57.8
	Trunk	86.2	13.8	89.4	2.4	8.2
	Roots	66.7	33.3	95.5	1.1	3.4
Autumn	New shoots	85.5	14.5	51.1	11.2	37.7
	Trunk	80.1	19.9	86.1	4.8	9.1
	Roots	73.6	26.4	91.0	1.9	7.1

trunk and cane, however, 17 per cent was found in the ethanol soluble fraction for the summer feeding, while it was 44 per cent for the autumn feeding. Of the ethanol soluble ^{14}C, 86–94 per cent was found in the soluble carbohydrates and only a small per cent in the organic and amino acids respectively, regardless of the feeding time or the plant part (Table 5).

At the flowering stage, 26–33 per cent of ^{14}C in the roots and 13–20 per cent of that in the trunk and cane were distributed in ethanol soluble fraction, of which around 90 per cent was found in the soluble carbohydrates. This was also true at the pruning time. While, in the newly developed shoots, 17–15 per cent of ^{14}C was distributed in the ethanol soluble fraction, which was halved into soluble carbohydrates and amino acids except for a small percentage which was distributed in the organic acids (Table 6).

Discussions

There seems little doubt that in most deciduous fruit trees no small amount of photosynthetic assimilates accumulates in the roots, trunk and canes, and is used as the source for the early growth of shoots in the following spring. However, from the quantitative viewpoint, sufficient data on the accumulation and retranslocation seems to be lacking. So far, many experiments have been performed with ^{14}C, which, in most cases, was supplied in the later part of the season. Thus, the autumn accumulated assimilates were shown to be distributed in a high ratio to the roots, next to the trunk and canes (branches and branchlets) in the vine (tree) just after pruning, or at the dormant stage (in grapevines, 1, 2; in apples, 3, 4, 5; in pecans, 6; etc.), though, in 'Muscat Alexandria' grapevines, only 30 per cent of ^{14}C was reported to be distributed to the roots (7).

In this report $^{14}CO_2$ was supplied to 'Delaware' grapevines in summer and autumn respectively. The percentage distribution of ^{14}C to the roots in the vine just after pruning was not only higher than that to the trunk and cane, but also higher for the autumn than for the summer feeding. Of course, in our experiments, $^{14}CO_2$ was supplied to a leaf or two on one of the two shoots, one of which was cut off at pruning. Consequently, it might influence the distribution pattern of ^{14}C whether or not the fed shoot was pruned off. Thus, when the total carbon is considered, the results obtained in Experiment II, in which the fed shoot was left as a fruit cane, seems to be closer to reality than those in Experiment I. In Experiment II, as much as 27 per cent was found in the cane for the summer feeding, but for the autumn feeding only 6 per cent was distributed to the cane and about 85 per cent was found in the roots as in Experiment I.

Respiratory consumption of ^{14}C during the period from pruning till the flowering stage was not measured due to technical difficulties. However, the respiratory consumption of ^{14}C during the shoot development on the basis of ^{14}C found in the vine just after pruning could be obtained by indirect calculation, the validity of

which, as compared with the direct one, will be shown in the following paper. In apples, more than 50 per cent of the autumn accumulated ^{14}C was calculated to be lost from the dormant to the flowering stage (3). In grapevines, our results indicated that the percentage respiratory consumption was higher for the autumn than for the summer feeding, being 24*–46 per cent and 18*–29 per cent respectively for the period from pruning till the flowering stage. This difference according to the feeding time seems to be related to the fact that much of the summer accumulated ^{14}C was incorporated into the constitutents of the plant body, while much of the autumn accumulated ^{14}C was stored as translocate reserves.

It appears that the retranslocation begins with the bud burst, although, in grapevines, some movement of the autumn accumulated ^{14}C within the roots was reported to occur during the bleeding stage prior to the bud brust (7). The most active retranslocation is generally seen in the earlier stages of shoot development, thus, in apples during the period from the bud burst till flowering (4) and in pecans during the initial leaf expansion stage (6). In grapevines in our experiments, it was during the period from the bud burst till the 6-leaf stage for the autumn feeding, while it was continued till the 10-leaf stage for the summer feeding. The maximum percentage retranslocation was 5.1**–5.2 and 15.3**–10.7 for the summer and autumn feedings, respectively, thus, the summer accumulated assimilates seem to be difficult to retranslocate both qualitatively and quantitatively as compared with the autumn accumulated ones. Moreover, the cessation of retranslocation was recognized between the 10-leaf stage and the flowering stage.

The magnitude of retranslocation was shown by several investigators. In apples, 7 per cent and 13–18 per cent of ^{14}C which had disappeared from the tree during the period from autumn till the establishment of the new shoot growth was recovered in the newly developed shoots (3, 4), and as the percentage retranslocation in our terminology the values of 4 and 6–8 per cent were calculated with their data. Conversely, the percentage recovery in the new shoots in our experiments was calculated at 20–30 per cent except for the autumn feeding in Experiment I, where it was over 60 per cent. In white pine trees, 5 per cent was reported as the percentage distribution to the newly developed shoots $11^1/_2$ months after ^{14}C application, when about 30 per cent of the initially assimilated ^{14}C was still present (8), and in mulberry trees, about 7 per cent as the percentage retranslocation to the new shoots 20–30 days after shoot pruning in summer (9). In grapevines, we obtained, as mentioned above, the values of 5.1–5.2 and 15.3–10.7 per cent as the maximum percentage retranslocation for the summer and autumn feedings respectively. Also, in another experiment reported later, a value of 9.2 was

*,** In Experiment I, the vines were pruned about two months later than Experiment II in the calendar date. If the pruning date were advanced by two months in Experiment I and in addition, the respiratory consumption during the two months weer assumed to be about 10 per cent according to Table 4, the figures in Experiment I would be modified as follows. *24→ 22, 18→ 16 **5.1→ 4.6, 15.3→ 13.4

obtained for ^{14}C accumulated throughout the growing season. Besides our data, the values of about 3 per cent and 60 per cent were reported separately as the percentage distribution to the new shoots at the shoot elongating stage (2) and the flowering stage (7) respectively. These values seem to be too small or too large when compared with ours. But the reason for such discrepancies is not known.

Within the newly developed shoot, there was found no distinctively active part as a sink till the 6-leaf stage as far as judging from RSS values and radioautographs, and even the flower cluster and shoot apex were not exception. After the 6-leaf stage, however, the degree of ^{14}C activity decreased from basal to apical leaves and from the base of the stem to its tip, and especially the apex showed almost no activity at the 10-leaf stage. These results seem to indicate that the early shoot development is dependent exclusively upon the retranslocated assimilates till the 6-leaf stage, but thereafter the current year assimilates exported from the lower leaves which obtain source ability begin to contribute to the shoot growth, while retranslocation gradually decreases till its cessation around the flowering stage.

At the flowering stage, 85 per cent of the ^{14}C in the newly developed shoots was found in the ethanol soluble fraction and considered to be incorporated into the constitutents of plant body. In the ethanol soluble fraction, ^{14}C was distributed in amino acids and soluble carbohydrates in equal ratio, different from the onesided distribution in soluble carbohydrates in the roots and trunk. In grapevines, nitrate reduction is reported to occur in the roots (10), and the high contents of amino acids in the vine including the roots before the bud burst are also known (11). Then, the amino acids found in the newly developed shoots seem to be retranslcoated after being synthesized in the roots. In our results, the ^{14}C in the amino acids in the roots and trunk was not high in its concentration but seemed to be sufficient in quantity to explain the retranslocation as amino acids instead of, or besides that as soluble carbohydrates (possibly as sucrose).

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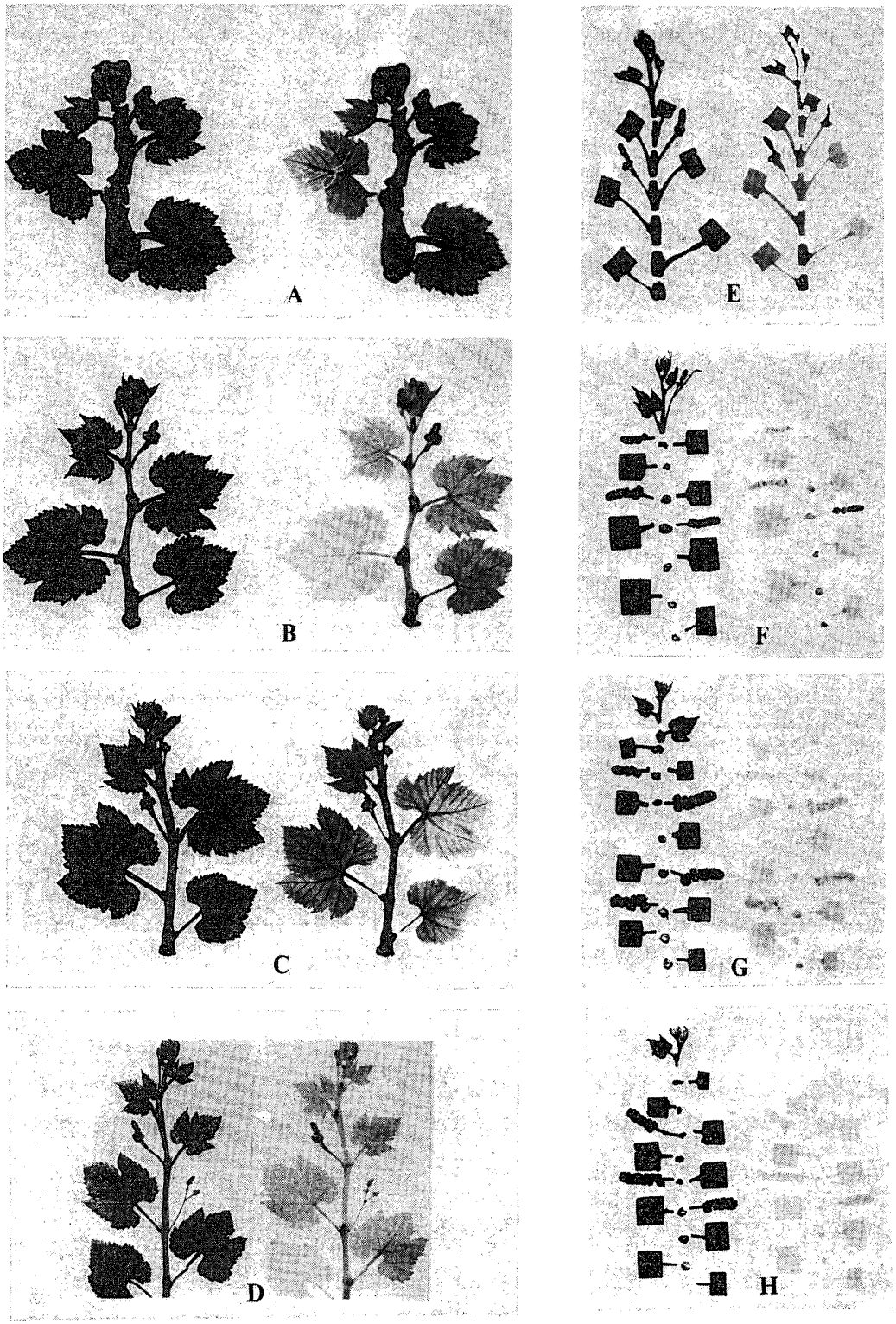

PLATE 1

PLATE 1. Distribution of ^{14}C-activity in the newly developed shoot in relation to its development.
Left: Mounted specimens. Right: Radioautographs. A–H: 3- to 10-leaf stage.